THE

AMERICAN NATURALIST.

VOL. XXXVIII. *October, 1904.* NO. 454.

THE ANATOMY OF THE CONIFERALES.

D. P. PENHALLOW.

(*Continued from page 554.*)

RESIN PASSAGES.

Distribution and Taxonomic Value.

PRANTL (44, p. 37) states that resin passages occur in the wood of "most Abietineæ, namely, Pseudotsuga, Picea, Larix, Pinus and *Abies firma*." This statement requires some modification in detail, especially with respect to the last named genus, and in order to make the results of the present studies clear it will be expedient to discuss separately the distribution of the resin cysts and the resin passages.

The first species to which our attention may be directed is *Tsuga mertensiana*. This is the only species of the genus in which definite resin cysts are to be found. Such structures are never numerous, and they take the form of short rows of contiguous cysts in the initial layer of the summer wood of distant growth rings. Longitudinally they have no definite limits, but they appear to be extended for great distances, and probably

through the entire longitudinal growth of the season, at least. There is no obvious alteration either in the position or volume of the resinous contents of the isolated resin cells which lie on the outer face of the summer wood. The constancy with which these structures occur gives to them a definite value for the recognition of the species, and permits us to differentiate it from *T. caroliniana* on the one hand and from the remaining three species on the other.

In the genus Abies only four species out of eleven show resin cysts. These are *A. bracteata*, *A. nobilis*, *A. concolor* and *A. firma*. Referring again to Prantl's observation (44, p. 37), it must be pointed out that his statement with respect to the occurrence of resin passages in *A. firma* requires modification in detail, in so far as these structures are not passages but cysts; while he also appears to have overlooked the occurrence of similar structures in the three other species mentioned. In all of these cases the cysts are contiguous and disposed in tangential rows of considerable length, either in the summer wood (*A. concolor* and *A. nobilis*), in the outer spring wood (*A. firma*), or in both the spring and summer wood (*A. bracteata*). Such variations appear to be of no specific value, conforming as they do to similar variations in the zonate distribution of the resin cells. It is found, however, that in only one case (*A. concolor*) are these cysts associated with isolated resin cells. In the three other cases the resin cells are entirely wanting, a relation which is strongly suggestive of their replacement by the cysts.

Sequoia sempervirens is the only species of that genus which develops resin cysts in the secondary wood, though Jeffrey (24) has shown that such structures are normal to the primary wood zone of *S. gigantea*, and not elsewhere. As already shown, such cysts are much more highly organized than those of either Tsuga or Abies, though they are similarly contiguous and even coalescent, and form extensive tangential rows in the initial layer of the spring wood of distant growth rings. They form a much more prominent feature than in any of the preceding species, because of their generally larger size and the greater extent of the series in which they lie. Unlike Abies, however, there appears to be no diminution either in the number or the extent

of the prominent resin cells which are often intimately associated with the cysts.

The normal course of development for such cysts as thus described is subject to special alteration under conditions which involve an unusual stimulus to growth, and under such circumstances they may become definitely associated with, or may even be regarded as indicative of, pathological conditions. Thus Anderson (1, p. 28–29) has shown that such cysts are definitely developed in association with the formation of Witches' brooms in *Abies firma.* Under such circumstances the cysts become much larger, more distant and more numerous than in normal growth, but they form well defined tangential rows in the earlier spring wood of successive growth rings. In the development of such secondary features the cysts manifestly exhibit a distinct approach to that higher type of structure and distribution which is exhibited in Picea. In the following year Anderson (2, p. 336) further showed that while resin cysts are absent from the normal wood of *A. balsamea* they do arise under the influence of the special stimulus connected with the formation of tumors produced by the action of *Æcidium elatinum.* He furthermore points out that such cysts attain their greatest development and largest number in the region of greatest stimulation, *i. e.*, in the middle of the tumor, decreasing above and below until they eventually become pointed and finally disappear between four tracheids "which, in their meristematic condition, probably function as epithelial cells." It is unfortunate that the histological details of these cysts and their endings are not given, since such facts would serve to throw much light upon the relation of the cysts to similar structures in normal tissues, but there is no reason to suppose that they differ in their essential structure from those which occur in the normal tissues of the same or other species. The tracheids above referred to are undoubtedly parenchyma tracheids, and it is probable that further examination would show that they ultimately replace the resin cells remaining over after the disappearance of the cyst proper.

More recently Jeffrey (24) has contributed an important paper on the anatomy of Sequoia in which he brings out several facts of considerable value. He shows that resin cysts may

arise in the roots of *Abies balsamea* which have been injured, while they may also be produced experimentally by injury, thus confirming the observations of Anderson that they may be traumatic in their origin. The most significant facts, however, relate to the normal occurrence of such cysts in Sequoia. He shows in the first instance that they are absent from the wood of the first year's growth in *Sequoia sempervirens*, while they are present for the same period of growth in *S. gigantea*, though absent from the growth of later years. In both species they arise in the earlier spring wood. Jeffrey concludes that the tangentially disposed resin cysts of *Sequoia sempervirens* represent the result of injury, and he would apply this rule to all similar cases in the various species of Abies and Tsuga.

Some years since, De Bary (9, pp. 490 and 495) formulated the law that "resin canals . . . . occur in the ligneous bundles of the same Abietineæ which possess horizontal canals in the medullary rays." This is a law of very great constancy, and, as recently shown by Penhallow (39), it is applicable without exception to all living species. But as the same author (41, p. 42) has shown more recently, *Sequoia burgessii* from the Eocene of the Northwest Territories offers a remarkable exception to this law, since it shows well defined resin passages in the medullary rays, but without corresponding structures in the vascular bundles.

As presented by existing species, Pseudotsuga, Larix, Picea and Pinus, without exception, show resin passages in both the radial and longitudinal positions. In transverse section they are scattered throughout, sometimes appearing chiefly in the summer wood, sometimes chiefly in the spring wood, or again about equally in the two regions, and they rarely conform to the precise law stated by De Bary (9, p. 495), that "they lie scattering in a ring in the external region of every annular layer." The constancy of their occurrence in the four genera mentioned involves very few features which call for special comment. In Pseudotsuga and Larix the resin passages are scattering. Sometimes they not infrequently unite in pairs so as to form short, tangential series and they thus approach the type of Tsuga or Abies, while yet again they may become definitely iso-

lated and scattering, thereby approaching the distribution of Picea and Pinus. In *Larix occidentalis* the tendency to a primitive form of distribution is expressed in the formation of a tangential zone essentially similar to that of *Tsuga mertensiana*. In both Pseudotsuga and Larix there is an obliteration of resin cells from all parts of the structure except the extreme outer face of the summer wood. In Picea, however, without exception, there is a complete obliteration of all resin cells except such as enter into the structure of the resin passages, and this is directly correlated with a higher type of structure in such passages.

In the genus Pinus, as already shown, the resin passage reaches the highest degree of organization in all respects. It shows little if any tendency to those primitive associations which are expressed in the formation of tangential series, while it has entirely replaced the isolated resin cells which are never to be found in that genus.

If, then, we ask what value such structures have for taxonomic purposes we find them to be of well defined importance. It has already appeared that in Tsuga the occurrence of resin cysts is of well defined value for specific differentiation, and the same rule is also applicable to *Sequoia sempervirens* and to four species of Abies. In the higher Abietineæ, inclusive of Pseudotsuga, Larix, Picea and Pinus, the invariable association of resin passages in the wood and in the medullary rays not only serves to separate these genera from all those in which resin cysts only may occur, but it differentiates them absolutely from all the remaining genera. Such association therefore constitutes a feature of great value. More particularly, the thin-walled epithelium of Pinus at once separates that genus from the other three, which are invariably characterized by thick-walled epithelium. Such generic differentiations are greatly emphasized by the occurrence of thyloses. These are typically developed in Pinus, where they are always thin-walled and almost invariably present. They are therefore of definite value as supplementing other features previously described. In the other genera, however, their presence in either the cyst or the resin passage, where they are generally thick-walled, is of so sporadic a nature as to give them no definite value, and we therefore find that for specific diagnoses such structures may be neglected.

Phylogenetic.

We are now in a position to present an answer to the question, "How are the resin passages related to the phylogeny of the Coniferales?" In order to present an intelligent answer to this question it will be necessary to recall the facts already discussed in connection with the resin cells and bring them into relation with our discussion of the resin passages.

In the genus Sequoia it has been shown that the general course of development of the resin cells is essentially the same as in Cupressus, etc., while it has also been shown that the genus presents in other respects a somewhat remarkable deviation. Of the two existing species, both show the distribution of the resin cells to be of the typically primitive form, *i. e.*, scattering. Nevertheless there are also in *Sequoia sempervirens* definitely organized resin cysts but without exhibiting the transitional form of a zonate disposition. Among fossil representatives Penhallow (41, p. 41) has shown precisely the same feature to be present in *S. langsdorfii*. This is the less remarkable, however, because that species is undoubtedly the ancestral form of, and practically identical with, *S. sempervirens*. The fact made clear by Jeffrey (24, p. 457), that resin cysts occur in the first annual ring of vigorous branches of adult trees, as well as in the roots of *S. gigantea*, also tends to make it apparent that the genus presents a very striking advance upon even the type presented by Juniperus, since the aggregation of resin cells and the formation of cysts from them has arisen abruptly and without the transitional forms presented by Juniperus and Taxodium. While, therefore, Sequoia is obviously related to Thuya and Cupressus on the one hand, it is on the other hand related to such types as Abies. In this sense it may be regarded as the terminal member of a developmental series embracing the Taxodiinæ, Cupressineæ, Taxoideæ as follows:—

1. Taxus and Torreya.
2. Thuyopsis.
3. Cryptomeria.
4. Podocarpus.

5. Cupressus.
6. Thuya.
7. Libocedrus.
8. Taxodium.
9. Juniperus.
10. Sequoia.

In the Abietineæ a new series is presented. This is not in any sense strictly coterminous with the first, but the two appear to make a fault, as it were, whereby there is a lateral displacement, but of such a nature that Sequoia still serves as the connecting link. Within the eleven species of Abies investigated three important phases are presented: (1) Resin cells scattering on the outer face of the summer wood, (2) resin cells grouped and forming cysts, and (3) resin cells entirely wanting. Viewing these phases in the order given, it is to be observed that in those four species which develop cysts only one shows isolated resin cells, and it is probably correct to interpret the variations noted as expressions of developmental phases in such a way that the occurrence of cysts represents the highest position. The genus Tsuga is closely related to Abies in the occurrence of isolated resin cells on the outer face of the summer wood, as also in the formation of resin cysts, but it obviously occupies an inferior position because (1) of the greater abundance of resin in the individual cells, and (2) the occurrence of definite aggregates of resin cells without the formation of cysts. This series is directly extended by those genera in which definite resin passages replace the simple cysts, since the latter are convertible into the former by easy and natural transitions. Both Pseudotsuga and Larix occupy equivalent positions because they not only present resin passages of an equal degree of development, but they show a survival of the isolated resin cells on the outer face of the summer wood. Their affinities are therefore directly with Abies and Tsuga on the lower side, but on the upper side their alliance is with Picea, which presents a very similar though somewhat higher organization of the resin passage and a complete obliteration of the isolated resin cell. Yet again, the structure of the resin passage in Picea at once connects that genus with

Pinus, in which the most complete development is attained, and it therefore terminates the series upwardly.

Having special reference to the particular forms of the secretory reservoirs, and leaving out of account all other considerations than their particular evolution, it is possible to indicate the general sequence of the genera and, to a more limited extent, of their species, as follows:—

1. Tsuga caroliniana.
   " mertensiana.
2. Abies bracteata.
   " firma.
   " nobilis.
   " concolor.
3. Sequoia.
4. Pseudotsuga and Larix.
5. Picea.
6. Pinus.

From this it is manifest that Sequoia is superior to Tsuga and Abies but inferior to Pseudotsuga, Larix, etc. But if we now view the general phylogeny with reference to the entire course of development of the resin cells and the resin passages, the relations just explained must be modified with reference to the particular position of Sequoia, and the sequence would then become:—

1. Thuyopsis and Cryptomeria.
2. Podocarpus.
3. Cupressus.
4. Thuya.
5. Libocedrus.
6. Taxodium.
7. Juniperus.
8. Sequoia.
9. Tsuga.
10. Abies.
11. Pseudotsuga and Larix.
12. Picea.
13. Pinus.

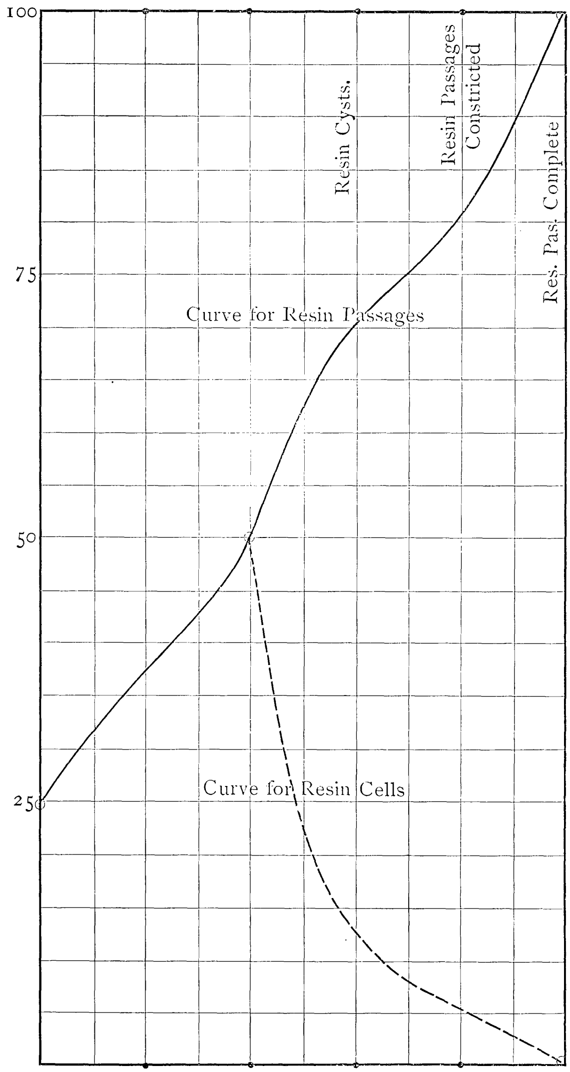
But it may assist in the general argument to view this question from another standpoint. Regarding the resin cells and the secretory reservoirs as falling within a definite series, we may apply to the various forms of distribution and to the various grades of resin reservoirs arbitrary values of such a nature as to represent our conception of their relative positions in the scale of development as expressed by percentages, thus: —

Resin cells scattering	25.0%
" " zonate	37.5 "
* " " grouped	50.0 "
" " on the outer face of the inner wood, Pseudotsuga and Larix . .	12.5 "
" " on the outer face of the summer wood, as in Abies (partial only),	5.0 "
" " wholly wanting	0.0 "
†Resin cysts, as in Tsuga, Abies and Sequoia .	70.0 "
Resin passages with constrictions, as in Pseudotsuga, Larix and Picea	80.0 "
Resin passages without constrictions and of the highest type of organization, as in Pinus .	100.0 "

We obviously have two subordinate series here, which for convenience may be regarded as coterminous, but which as already shown are "faulted" in such a way that the grouped resin cells (*) and the resin cysts (†) jointly represent the point of divergence for two separate courses of development, the latter continuing upward, while the former descends and thereby represents degradation. These features are best exhibited graphically, and the accompanying curves clearly show how, on the one hand, resin cysts and resin passages directly result from special modification of cell aggregates, while on the other hand, from the same starting point, there arises a course of degradation which finally results in the complete obliteration of the resin cell as an independent structure.

The facts thus far set forth have thrown important light upon the general course of development of certain anatomical features, and they also show the general course of development for genera

and species with reference to particular structures. They do not, however, convey any information with respect to the origin



Curve showing the approximate development of resin passages, and the corresponding obliteration of resin cells.

of the phylum as a whole, or the relations of the particular gënera and species from the standpoint of collective data, and such a

discussion will be more appropriately reserved for the general summary. There is, however, one feature arising out of recent investigations which calls for consideration at this point, since certain of the conclusions reached are not in harmony with our own, the divergence of opinion indicated being the result of different methods of interpretation.

Jeffrey states (24, pp. 447 and 457) that *all* such resin cysts as occur in *Sequoia sempervirens* and Abies are of a traumatic nature, and therefore pathological. To this category he would also doubtless assign the corresponding structures of Tsuga. This opinion appears to be shared by Anderson (1 and 2), and it is also apparently supported by Pierce (42). Both Jeffrey and Anderson show that the development of such cysts is sometimes definitely associated with the production of tumors through the operation of parasites, and that they may also be induced by wounds experimentally produced. The facts they cite show conclusively that resin cysts may, and often do, arise traumatically, but in such cases they lie outside the usual course of development.

The occurrence of resin passages in the fundamental tissue of the Coniferales is a well known fact, as pointed out by De Bary (9, p. 441) many years since, when he summarized the general facts in the statement that "all investigated species of Coniferæ, with the single exception of Taxus, have resin passages or resin reservoirs which vary in distribution and number according to the species." This statement would include the leaves and bark and sometimes even the pith of species which produce neither isolated resin cells nor resin reservoirs of any kind in the xylem tissue of the stem. It directs attention somewhat forcibly to the fact that while the occurrence of resin reservoirs in the fundamental tissue is a legitimate inheritance of the mucilage canals of the Eusporangiate ferns and the Cycadofilices, as also later of the resin cells of Cordaitales, the xylem structure is the very last to receive the impress of such a course of development; and it is therefore in nowise surprising that the resin passages do not appear there until a very late period of development and that their organization can even then be brought about only through a somewhat prolonged series of changes which are initiated by the occurrence of isolated resin

cells, much as the formation of mucilage canals may be traced back to specialized cells which separately have the same function in the Eusporangiate ferns.

The local occurrence of resin passages in the xylem of the floral axis in no way invalidates the obvious conclusions to be drawn from these statements, since it may be readily accounted for in other ways. In a structure so unresponsive to influences which would induce profound alterations as the xylem, it is to be expected that important structural changes could be effected only after a prolonged interval during which the fixation of any particular character would be preceded by a period of sporadic development within which such character would be liable to recur under special conditions; and as such conditions are obviously of fundamental importance we may inquire somewhat more fully into their nature and results.

The statement of Prantl (44, p. 35) that "those genera which are devoid of resin passages in the wood of young and vigorous growth later produce single parenchyma elements in the wood, which contain resin" requires some modification in view of what Jeffrey has shown in the case of Sequoia and Abies, as well as what has been shown in the course of the present studies, and in its more comprehensive and exact form it should read, "those genera which are usually devoid of resin passages in the wood, but some species of which may nevertheless contain resin cysts in the young and vigorous growth, later produce single parenchyma elements in the wood, which contain resin."

Taken by itself this statement as applied to Sequoia and Abies might be held to indicate that the growth of the first year represents the most stable structural region of the entire stem, in the sense that it embodies characters which are most fully established, and that it will therefore embrace elements which may be eliminated from the older parts, or which may be replaced there by degenerate forms only. From this point of view it would be necessary to regard the complex resin passage as the primitive form of structure from which the cysts, groups of cells and isolated resin cells have been derived by a process of progressive degradation. This view appears to have been

adopted by Jeffrey (24, p. 454), who supports his position by citing the occurrence of resin passages in the vascular structure of the peduncle of certain fossil Cycads, interpreting this to mean that such structures represent a survival of features which have been obliterated from the structure of the stem. Such a view does not seem to be in harmony with the facts which our own studies have brought out, to the effect that resin passages of the type found in the xylem structure are in no sense primitive or vestigial, since they are wholly wanting in the primitive gymnosperms, and their organization does not arise until a very late period in the evolution of the highest forms. If our interpretation of observed facts is correct as applied to the origin of the resin passages, it shows as clearly as one could well expect a progressive development from the isolated resin cell through various phases of aggregation to the highest form of structure as found in Pinus. That there is such a series cannot be doubted and we must interpret it in one of two ways: either as progressive evolution or as progressive degeneration. To us the arguments all seem to be very emphatic with respect to lending support to the former view, most especially as all anatomical data confirm the relative positions of the genera as determined by the development of the resin passage. But assuming for the moment that the latter view is the correct one, let us see where it would lead us. It would first of all necessitate a direct reversal of the structural sequence, and this in turn would impose the necessity of placing the genus Pinus at the bottom of the scale, while those genera like Taxus, Torreya, Agathis, etc., which have no resin cells even, would be at the top. I venture to suggest that such a proposition would meet with instant opposition even from the advocates of the idea that the resin passage has preceded the other forms of resin bearing structures. The whole question appears to turn upon our recognition of what constitutes the most impressionable portions of the stem structure, and therefore the regions within which structural changes are initiated. In this connection the evidence of both palæobotany and recent botany brings out certain facts with great force and throws them into strong relief. They are as follows:

1. The mucilage canals of the Eusporangiate ferns may be regarded as the ancestral forms of the resin passages among the higher plants, but they are obviously the successors of, as they are derived from aggregates of, mucilage sacs as simple, parenchyma cells.

2. Resin passages are wholly unknown in the wood of the stem of ferns, the Cycadofilices, the Cycads, Cordaites or Araucarioxylon.

3. Resin cells are known and are abundant in the pith and bark of Cordaites, but they are absent from its wood.

4. Resin passages are known in the bark and in the pith of the Cycadaceæ, of Agathis, Araucaria and of the Coniferales in general. They also occur in the wood of the peduncles of Sequoia and Cycas, and in the xylem of the first year's growth of vigorous shoots in Sequoia and Abies. They likewise occur in the leaves generally.

5. In *Sequoia burgessii* from the Eocene, resin passages occur in the medullary rays, but they do not traverse the wood longitudinally, though isolated resin cells do occur there.

From this it would seem that the fundamental tissue is the most impressionable with respect to the development of these structures, and that after it we have in the same order the peduncle of the inflorescences and the wood of the young shoots, to which latter category would also belong the development of resin passages in fasciated stems, and such a sequence is precisely what we should expect from our knowledge of the relation which the fundamental tissue bears to other structures. According to this conception the resin passages may appear in any part of the woody structure where growth is sufficiently vigorous, but such appearance would be temporary and indicative only of a future course of development which has not as yet become sufficiently well impressed upon the organism to form a permanent feature of it. In other words, the tissue exhibits what in other cases would be termed "sports." Such structural forecasts are well known and of frequent occurrence and as applied to the development of tissues no better example is afforded than that shown by the central strand of mosses, which is generally accepted as prophetic of the future vascular system

in the sporophyte. They serve to suggest that the law of mutation as proposed by De Vries finds expression in the evolution of internal structures as well as in the development of external forms. Such cases as *Sequoia gigantea,* which shows resin cysts in the wood of the first year and nowhere else, being replaced later by resin cells, appear to us to show that young and vigorous growth in general, and therefore the growth ring of the first year, constitutes a transitional zone within which many changes of structure wholly apart from the strictly normal may arise; and such a law would similarly be applicable to the wood of peduncles. This feature is manifested in the structure of the medullary ray, the character of the tracheids as exhibited in transverse section, the genesis of the bordered pits from spiral tracheids, and in all probability also in the formation of resin passages in Sequoia and Abies as noted by Jeffrey.

Changes of this nature are to be regarded as tendencies in development in the direction of higher types of structure whereby potentialities assume a more or less definite form. From this it may be assumed that the primary growth ring is a zone within which sporadic characters are common, but it is only in the later rings that the various anatomical characters become permanently developed and properly express the normal features of structure and development.

This view is justified not only by observed facts but also by analogy which shows that as plants ascend in the scale they exhibit sporadic characters or "sports" as tendencies toward the development of otherwise potential characters. As plants gain in complexity such tendencies become manifested not simply in alterations of external form but with respect to particular details of structure and development. We therefore find ourselves compelled to conclude that the development of resin cysts and resin passages from resin cells, and the occurrence of the latter in the Coniferales, shows that all of these structures are features in the development of higher types of plants, and it is difficult for us to accept the statement of Jeffrey that such resin passages represent primitive structures and are of the nature of survivals.

Returning to the question of the traumatic nature of the

resin cysts in Sequoia, Abies and Tsuga, which Jeffrey appears disposed to formulate as a general law, it is not clear to us how this can be made to harmonize with facts coming under our own observation. It has been shown that such resin cysts occur in one species of Sequoia, four species of Abies and one species of Tsuga, yet another species of which also shows them in a potential form. The same elements appear in each case, *viz.*:—

1. The cysts assume a definite form in distribution.

2. They always occupy a definite place in the scale of structural organization.

3. They are constant features of the same species.

4. They occur at frequent intervals in the same transverse section, showing them to be repeated at intervals of from one to several years.

It is exceedingly difficult to conceive how injuries could be inflicted upon particular species with such constancy, and in such a way as to produce uniform results in the production of resin cysts which occupy a definite place in the structural scale.

It is a well known fact in the physiology of plants, that conditions which induce a premature development of parts also bring about the conversion of potentialities into actualities, and under such circumstances the latter become evidences of a pathological condition. The swamp maple normally develops a brilliant foliage in the autumn, but it is not uncommon to find individual branches which have been injured, or even entire trees, which exhibit the characteristic autumnal foliage in midsummer, a condition which is correctly interpreted as pathological. Special conditions of nutrition, *e.g.*, an excess of mineral food elements, may similarly induce a premature development of the reproductive process. It has been shown by Richards that in cases of injury the rate of respiration is greatly increased, an alteration in functional activity which he rightly interprets as due to efforts directed toward the repair of injured parts. But this implies a local increase of nutritive materials and their application to a more intensive process of nutrition. Such features are well known in the case of all hypertrophies, and they must be similarly applicable to all forms of wounds, no matter what their origin, differing only in degree. We cannot

very well conceive of such profound functional disturbances without assuming a corresponding alteration in or development of those structures upon which the activities are dependent. The structural alterations may thus become characteristic, *local* features, and they may even represent the tangible expression of potentialities which are not manifested elsewhere in similar regions of the plant body. Furthermore, normal resin canals are invariable features of Larix, Pseudotsuga, Picea and Pinus. But Anderson (1, p. 29, etc.) has shown that in *Picea axcelsa*, *Larix japonica* and *Pinus strobus* there is an enormous increase in the number of resin canals, arising through the unusual stimulus afforded by the operations of the mycelium of *Agaricus melleus*. With respect to *Abies firma* he also clearly shows that the general effect of the stimulus afforded by the parasite *Æcidium elatinum* (which gives rise to hexenbesen) is to produce a more perfectly organized form of the secretory reservoir than is present under normal conditions. To us, therefore, these facts offer a reasonable explanation of the appearance of resin cysts under conditions of injury, when they assume a pathological rôle, while they also serve to harmonize their occurrence under such circumstances with the general course of their evolution as already set forth.[1]

The results to which we are now brought are based entirely upon developmental phases in anatomical elements of the vascular cylinder. While our studies lead us to certain definite conclusions, we do not in any sense regard the latter as final, but only as affording one step in the solution of a question which must be viewed not only from the broader standpoint of more extended anatomical data, but from that of Physiology as well, although we feel disposed to insist that the final answer will be found to rest chiefly upon an anatomical basis. That there may be room for a different interpretation of the facts here recorded, is quite possible, since Dr. Jeffrey has recently permitted me to

[1] Since the above was written, Dr. Jeffrey has very kindly shown me several specimens which appear to afford strong evidence in support of his position, and in view of such facts the conclusions here stated are made with reserve until further evidence is at hand through the publication by him of studies now in progress.

examine the manuscript of an important contribution to our knowledge of the Abeitineæ, in which he brings out very significant facts suggestive of the idea that this group is of a much more primitive character than has hitherto been supposed, or than is indicated by our own studies. It is therefore of importance that final judgment should be suspended until the results of these various studies, as well as those of Coulter and Chamberlain, all directed to the same end but prosecuted along entirely distinct lines, can be brought together and co-ordinated. It is in this sense, therefore, that we offer the following.

SUMMARY AND GENERAL CONCLUSIONS.

In discussing the phylogeny of the higher Gymnosperms, three subordinate phyla must be taken into consideration in the following order:—(1) Cordaitales, (2) Ginkgoales, (3) Coniferales.

Regarding the Cordaitales as the most primitive gymnospermous stock of which we have present knowledge, it is possible to trace its origin to the Cycadofilices. The genera Lyginodendron, Heterangium, Calamopitys and Pityoxylon present many structural features which are common to all, and which not only establish their relation to the Cycadean line of descent, but they offer many suggestions of that course of development which is realized in the higher Coniferales. They therefore constitute the real starting point for two lines of descent, the first of which embraces the Cycadales. With this we have little or nothing to do at the present moment, beyond establishing its probable relation to the other gymnosperms. The second line emerges in a type of plants having characteristics distinctly allied to those of the Coniferæ, and it is this line of descent with which we are now chiefly concerned. It is now possible to define the origin of this phylum somewhat more exactly than Coulter has done (7 & 8), since there is good reason to believe that it emerges from the Cycadofilices through Poroxylon. Scott (52, p. 398) has already pointed out the relations of this genus to the Cycadofilices and the Cycadaceæ on the one hand, and to Cordaites on the other, so clearly as to remove the necessity for detailed

discussion at this time, beyond giving emphasis to one or two important structural relations. It has been noted that in *Calamopitys saturni*, the most primitive distribution of the bordered pits upon both the radial and tangential walls, is represented in the protoxylem structure. Such distribution, however, undergoes rapid modification whereby it is wholly limited to the radial walls in the secondary wood. A similar limitation appears in other, somewhat closely related genera, and it is fully expressed in Poroxylon where the multiseriate disposition and hexagonal form are typically preserved, though there is, at the same time, a tendency to segregation to such an extent that the pits sometimes become round. In this it is possible to notice the first indication of a character which, while infrequent, is nevertheless occasionally expressed among the Cordaitales, though it is generally characteristic of the related phyla Ginkgoales and Coniferales.

Among the Cordaitales there is but one genus (Cordaites) which we have heretofore been accustomed to associate with that phylum, and, so far as our present knowledge goes, it undoubtedly stands in the closest relations to Poroxylon. It is, however, improbable that the two were in any sense coterminous, and it is altogether probable that there may have been some one or more intermediate forms of which we have no present knowledge. Our present studies on the other hand, show clearly, that we must bring into this phylum two other genera of an obviously higher degree of development, but which have commonly been ranked with the Abietineæ and which, according to Eichler (11), occupy the highest position in the scale. This position is untenable upon anatomical grounds which give us reason to believe that Agathis and Araucaria (including, of course, Araucarioxylon) are not only inferior to the Coniferales as a whole, but that they are distinctly Cordaitean. Accepting this view, and the fact that Agathis is the inferior genus, the sequence would place Cordaites at the base and Araucaria at the top, with Walchia as the immediately ancestral form of the latter. This relation is not only natural, but it is justified on anatomical grounds.

The tendency to segregation of the bordered pits as exhibited by Poroxylon suggests the relation of this genus to others in

which such a feature is fully expressed, and it thereby forms the basal member of another series. From the opposite point of view, it has been shown that the occurrence of two-seriate pits in Pinus and others of the Coniferales, as well as in Ginkgo, points to a common origin for such genera in a type with multiseriate, hexagonal pits, and that both Agathis and Araucaria must likewise center in the same generalized form. This gradual convergence is justified on other grounds, and the genus Poroxylon among known forms most nearly fulfills the requirements of the case. We may therefore look upon it as lying between the Cycadofilices and all the higher gymnosperms, giving rise to two lines of descent, the first of which embraces the Cordaitales as already described, while the second shortly divides once more. This secondary division gives rise on the one side to the Ginkgoales, and on the other to the Coniferales. The anatomical data already discussed when viewed collectively show that the general sequence within the latter would be (1) the Taxoideæ, (2) the Taxodiinæ, (3) the Cupressineæ, (4) Abies, (5) Tsuga, (6) Pseudotsuga, (7) Larix, (8) Picea and (9) Pinus, of which one division (II) represents the highest type of development. The sequence of species for each genus cannot always be determined with a full measure of satisfaction, and these difficulties may possibly be made clear by reference to a particular case. The succession of the two species of Sequoia is difficult to determine on purely anatomical grounds, but the general tendency of the facts already recited is to give to *S. sempervirens* the more primitive position, a view which is sustained by its palæontological history.

The relations brought out in the foregoing studies, and the conclusions reached, may be made more obvious without the tedious method of a detailed discussion by reference to the accompanying table of anatomical data, which substantially summarizes all the results derived from the study of particular structures.

Data for Table of Anatomical Characters, in identical series.

1. Spiral tracheids.
2. Bordered pits in 1–3 rows.
3. Bordered pits in 1–2 rows.
4. Bordered pits in one row.
5. Pits on the tangential walls of the summer wood.
6. Lateral walls of the ray cells with bordered pits.
7. Uniseriate rays.
8. Terminal walls of the ray cells thin and entire.
9. Resin cells.
10. Terminal walls of the ray cells locally thickened.
11. Terminal walls of the ray cells strongly pitted.
12. Ray tracheids.
13. Resin passages.
14. Fusiform rays.
15. Thyloses in the resin passages.
16. Lateral walls of the ray cells with simple pits.
17. Ray cells of two kinds.

1. Resin cells scattering.
2. Resin cells zonate.
3. Resin cells grouped.
4. Resin cells on the outer face of the summer wood.
5. Ray tracheids marginal.
6. Ray tracheids interspersed.
7. Ray tracheids dentate.

A. Number of species.
B. Percentage value of genus.

TABLE OF ANATOMICAL CHARACTERS OF THE CORDAITALES, GINKGOALES AND CONIFERALES.

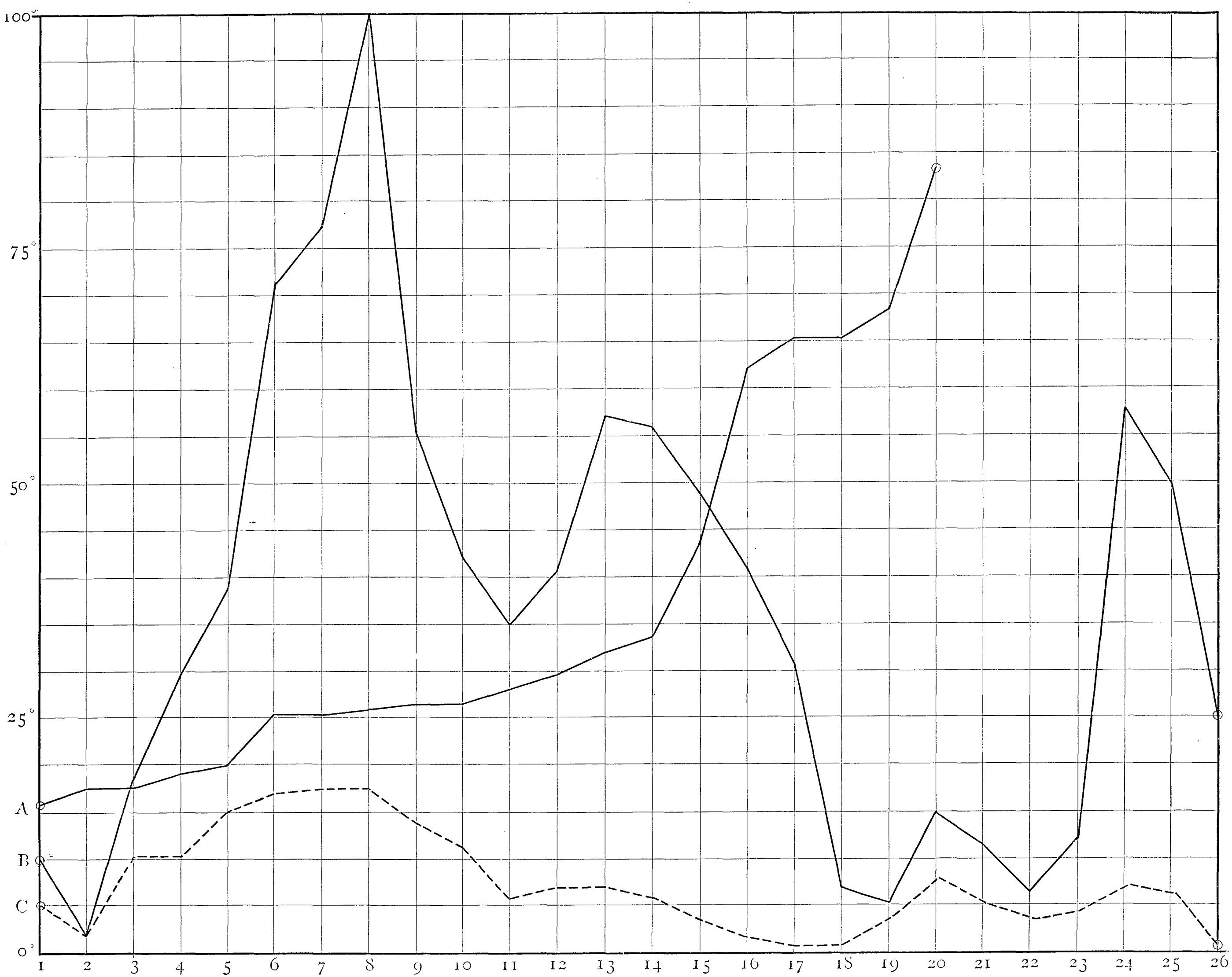
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	1	2	3	4	5	6	7	A	B
1 Agathis australis.	—	×			×	×	×	×																	1	16.
2 Araucaria cunninghami.	—	×			—	×	×	×																	3	17.7
excelsa.	—	—	×		—	×	×	×																		
bidwillii.	—	—	—	×	—	×	×	×																		
3 Ginkgo biloba.	—	—	×		×	×	×	×																	1	17.7
4 Torreya taxifolia.	×	—	×		—	×	×	×																	3	19.0
californica.	×	—	—	×+	×	×	×	×																		
nucifera.	×	—	—	×	—	×	×	×																		
5 Taxus floridana.	×	—	—	×—	×	×	×	×																	4	19.9
canadensis.	×	—	—	×	×	×	×	×																		
brevifolia.	×	—	—	×	×	×	×	×																		
cuspidata.	×	—	—	×	×	×	×	×																		
6 Thujopsis dolabrata.	—	—	—	×	×	×	×	×	×									×							1	25.4
7 Cryptomeria japonica.	—	—	—	×	×	×	×—	×	×									×							1	25.4
8 Podocarpus macrophylla.	—	—	—	×	×	×	×	×	×									×	(o)						1	25.9
9 Taxodium distichum.	—	—	(1)	×	×	×	×	×	×									(1)	×						1	26.4
10 Libocedrus decurrens.	—	—	—	×+	×	×	×	×	×	(o)								(1)	×						1	26.4
11 Thuya gigantea.	—	—	—	×+	×	×	×	×	×										×						3	28.2
occidentalis.	—	—	—	×+	×	×	×	×	×									×	(o)							
japonica.	—	—	—	×+	×	×	×	×	×			×						×				×				
12 Sequoia sempervirens.	—	—	×		×	×	×	×	×				×—		×			×		×					2	29.7
gigantea.	—	—	×		×	×	×	×	×									×								
13 Cupressus lawsoniana.	—	—	(1)	×	×	×	×	×	×									×	×						9	32.0
pisifera.	—	—	—	×+	×	×	×	×	×										×							
obtusa.	—	—	—	×	×	×	×	×	×									×	×							
macrocarpa.	—	—	—	×+	×	×	×	—	×	×								×	(o)							
arizonica.	—	—	—	×	×	×	×	—	×	×								×		×						
macnabiana.	—	—	—	×	×	×	×	—	×	×									×							

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	1	2	3	4	5	6	7	A	B
13 Cupressus goveniana.	—	—	—	×	×	×	×	—	×	×								×								
thyoides.	—	—	(1)	×	×	×	×	—	×	×		×						×	(0)			×				
nootkatensis.	—	—	—	×	×	×	×	—	×	×		×						×	×			×				
14 Juniperus virginiana.	—	—	—	×+	×	×	×	—	×	×								—	×						11	33·4
nana.	—	—	—	×	×	×	×	—	×	×		(1)						—	×							
rigida.	—	—	—	×	×	×	×	—	×	×								—	×							
californica.	—	—	—	×	×	×	×	—	×	×	(0)							—	×							
utahensis.	—	—	—	×	×	×	×	—	×	×	(0)							—	×							
sabinoides.	—	—	—	×	×	×	×	—	×	×	(0)							—	×							
communis.	—	—	—	×	×	×	×	—	×	×	(0)							—	×							
sabina.	—	—	—	×	×	×	×	—	×	×	(0)							—	×							
pachyphloea.	—	—	—	×	×	×	×	—	×	—	×							(1)	×							
monosperma.	—	—	—	×	×	×	×	—	×	—	×								×							
occidentalis.	—	—	—	×	×	×	×	—	×	—	×								×							
15 Abies fraseri.	—	—	—	×+	×	×	×	—	—	—	×							—	—						11	43·5
lasiocarpa.	—	—	—	×	×	×	×	(1)	—	—	×							—	—							
veitchi.	—	—	—	×	×	×	×	—	—	—	×							—	—							
balsamea.	—	—	(1)	×	×	×	×	—	—	—	×	×						—	—	—	×	×				
magnifica.	—	—	—	×	×	×	×	—	×	(1)	×							—	—	—	×					
amabilis.	—	—	—	×+	×	×	×	—	×	—	×							—	—	—	×	×				
grandis.	—	—	—	×	×	×	×	—	×	(1)	×							—	—		×	×	×			
bracteata.	—	—	(1)	×	×	×	×	×	×	—	×		×—					—	—	×						
nobilis.	—	—	—	×+	×	×	×	—	×	—	×		×—					—	—	×						
concolor.	—	—	—	×	×	×	×	—	×	×	(1)		×—		×			—	—	×	×					
firma.	—	—	(:)	×	×	×	×	—	×	—	×		×—					—	—	×						
16 Tsuga canadensis.	—	—	×		×	×	×	—	×	—	×—	×						—	—	—	×	×	×		5	62.2
sieboldii.	—	—	—	×+	×	×	×	—	×	—	×	×						—	—	—	×	×	×			
caroliniana.	—	—	—	×	×	×	×	—	×	—	×	×						—	—	×	×	×				
pattoniana.	—	—	—	×	×	×	×	—	×	—	×	×						—	—	—	×	×	(0)			
mertensiana.	—	—	—	×	×	×	×	—	×	—	×	×	×—					—	—	×	×	×				

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	1	2	3	4	5	6	7	A	B
17 Pseudotsuga douglasii.	×	—	—	×+		×	×	—	×	—	×	×	×	×				—	—	—	×	×	(o)		2	65.2
macrocarpa.	×	—	—	×	×	×	×	—	×	×		×	×	×				—	—	—	×	×	(o)			
18 Larix occidentalis.	—	—	×		×	×	×	—	×	—	×	×	×	×				—	—	—	×	×			4	65.2
americana.	(1)	—	×		×—	×	×	—	×	—	×	×	×	×				—	—	—	×	×	(o)			
lyallii.	—	—	—	×+	×	×	×	—	×	—	×	×	×	×				—	—	—	×	×	(o)			
leptolepis.	—	—	—	×	×—	×	×	—	×	—	×	×	×	×				—	—	—	×	×	(o)			
19 Picea breweriana.	—	—	—	×	×	×	×	—	—	—	×	×	×	×				—	—	—	—	×			10	68.5
rubra.	—	—	—	×	×	×	×	—	—	—	×	×	×	×				—	—	—	—	×	(o)			
alba.	—	—	—	×	×	×	×	—	—	—	×	×	×	×				—	—	—	—	×	(o)			
engelmanni.	—	—	—	×	×	×	×	—	—	—	×	×	×	×				—	—	—	—	×				
jesoensis.	—	—	—	×	×	×	×	—	—	—	×	×	×	×	(1)			—	—	—	—	×	(o)			
polita.	—	—	—	×+	×	×	×	—	—	×	—	×	×	×	(1)			—	—	—	—	×	(o)			
bicolor.	—	—	—	×	×—	×	×	—	—	(1)	×	×	×	×	(1)			—	—	—	—	×	×			
pungens.	—	—	—	×	×	×	×	—	—	—	×	×	×	×	(1)			—	—	—	—	×	(o)			
nigra.	—	—	—	×	×	×	×	—	—	—	×	×	×	×	×			—	—	—	—	×	(o)			
sitchensis.	—	—	—	×	×	×	×	—	—	—	×	×	×	×	×			—	—	—	—	×	(o)			
20 Pinus. Sec. I.																										
parryana.	—	—	—	×	×	×	×	—	—	×	(1)	×	×	×	×			—	—	—	—	×	(o)		41	83.3
cembroides.	—	—	—	×	×	×	×	—	—	(1)	×	×	×	×	×			—	—	—	—	×	(o)			
monophylla.	—	—	—	×	×	×	×	—	—	—	×	×	×	×	×			—	—	—	—	×	×			
balfouriana.	—	—	—	×	×	×	×	—	—	—	×	×	×	×	×			—	—	—	—	×	(o)			
aristata.	—	—	—	×	×	×	×	(1)	—	—	×	×	×	×	×		×	—	—	—	—	×	(o)			
edulis.	—	—	—	×	×	×	×	(1)	—	—	×	×	×	×	×		×	—	—	—	—	×	(o)			
lambertiana.	—	—	×		×	—	×	×	—	(1)	—	×	×	×	×	×		—	—	—	—	×	(o)			
monticola.	—	—	—	×+	×	—	×	×	—	(1)	—	×	×	×	×	×		—	—	—	—	×	×			
flexilis.	—	—	—	×	×	—	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	(o)			
reflexa.	—	—	—	×	×	—	×	×	—	(1)	—	×	×	×	×	×		—	—	—	—	×	(o)			
strobus.	—	—	—	×	×	—	×	×	—	(1)	—	×	×	×	×	×		—	—	—	—	×	(o)			
parviflora.	—	—	—	×	×	—	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	(o)			
albicaulis.	—	—	—	×	×	—	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	(o)			

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	1	2	3	4	5	6	7	A	B
20 Pinus. Sec. II.																										
clausa.	—	—	×		—	×	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	×	×		
rigida.	—	—	—	×+	—	×	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	(o)	×		
serotina.	—	—	(1)	×+	—	—	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	×	×		
banksiana.	—	—	(1)	×	—	—	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	×	×		
contorta.	—	—	—	×+	—	—	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	(o)	×		
glabra.	—	—	—	×	—	—	×	×	—	—	—	×	×	×	×	×	(1)	—	—	—	—	×	×	×		
echinata.	—	—	—	×+	—	—	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	×	×		
resinosa.	—	—	—	×+	—	—	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	(o)	×		
koraiensis.	—	—	—	×+	—	(1)	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	(o)	×		
thunbergii.	—	—	—	×	—	(1)	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×		×		
densiflora.	—	—	—	×	—	(1)	×	×	—	—	—	×	×	×	×	×		—	—	—	—	×	(o)	×		
murrayana.	—	—	—	×+	—	(1)	×	×	—	×	—	×	×	×	×	×		—	—	—	—	×	×	×		
arizonica.	—	—	—	×+	—	—	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
coulteri.	—	—	—	×+	—	—	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×		×		
tuberculata.	—	—	—	×+	—	(1)	×	×	—	×		×	×	×	×	×	×	—	—	—	—	×	×	×		
torreyana.	—	—	—	×+	—	—	×	×	—	×		×	×	×	×	×	×	—	—	—	—	×	(o)	×		
chihuahuana.	—	—	—	×+	—	—	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
jeffreyi.	—	—	—	×+	—	—	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
ponderosa.	—	—	—	×	—	—	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
scopulorum.	—	—	—	×	—	—	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
pungens.	—	—	—	×+	—	×	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
inops.	—	—	—	×+	—	(1)	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
muricata.	—	—	—	×+	—	—	×	×	—	—	×	×	×	×	×	×	×	—	—	—	—	×	×	×		
insignis.	—	—	—	×+	—	—	×	×	—	—	×	×	×	×	×	×	×	—	—	—	—	×	×	×		
sabiniana.	—	—	×		—	—	×	×	—	×	—	×	×	×	×	×	×	—	—	—	—	×	(o)	×		
tæda.	(1)	—	×		—	—	×	×	—	—	—	×	×	×	×	×	(1)	—	—	—	—	×	×	×		
palustris.	—	—	×		—	—	×	×	—	—	—	×	×	×	×	×	×	—	—	—	—	×	×	×		
cubensis.	—	—	×		—	—	×	×	—	×	×	×	×	×	×	×	×	—	—	—	—	×	×	×		

In preparing this table, the various anatomical features have been chosen with reference to (1) the constancy of their occurrence, (2) their structural prominence and (3) their obvious relation to diagnostic purposes. In their horizontal extension, an attempt has been made to arrange them in accordance with the law of frequency, as well as with reference to their relation to development, in such wise that while the spiral tracheid is assumed to be the most primitive type of the vascular structure, the presence of two kinds of cells in the medullary ray may be held to express the highest form of development. To the members of the series so constituted we may then assign arbitrary values in arithmetical sequence from one to seventeen ; while those subordinate characters which are represented by different forms of distribution may be regarded as forming a second series similarly valued. Any primitive or other character which has become obliterated through development may be held to retain its original value with respect to the general course of such development, and it is always indicated by —. Vestigial structures occurring sporadically are designated by (1), and to them one half the value of the fully developed character is assigned. All normal features are designated by ×, which becomes × + when they show development toward the next higher form, or by × — when they show a definite tendency to degeneration. Sporadic characters which are obviously in the line of development are indicated by (o), but they are assigned only half values. On this basis it is possible to arrange a sequence of genera and species in such a manner as to exhibit a progressive development from the simple Agathis with a minimum of characteristics to the complex Pinus in which the greatest number of anatomical features are involved. Furthermore, through such a series it is possible to determine the relative position of the various genera by percentage values, and this gives the most valuable insight into the approximate relations of the various members within the general line of descent. Such relations are determined not only for each anatomical character, but for the collective characters. Reducing these facts to a graphic form, the accompanying curves will assist in making the relations more clear, especially in emphasizing the general course of develop-

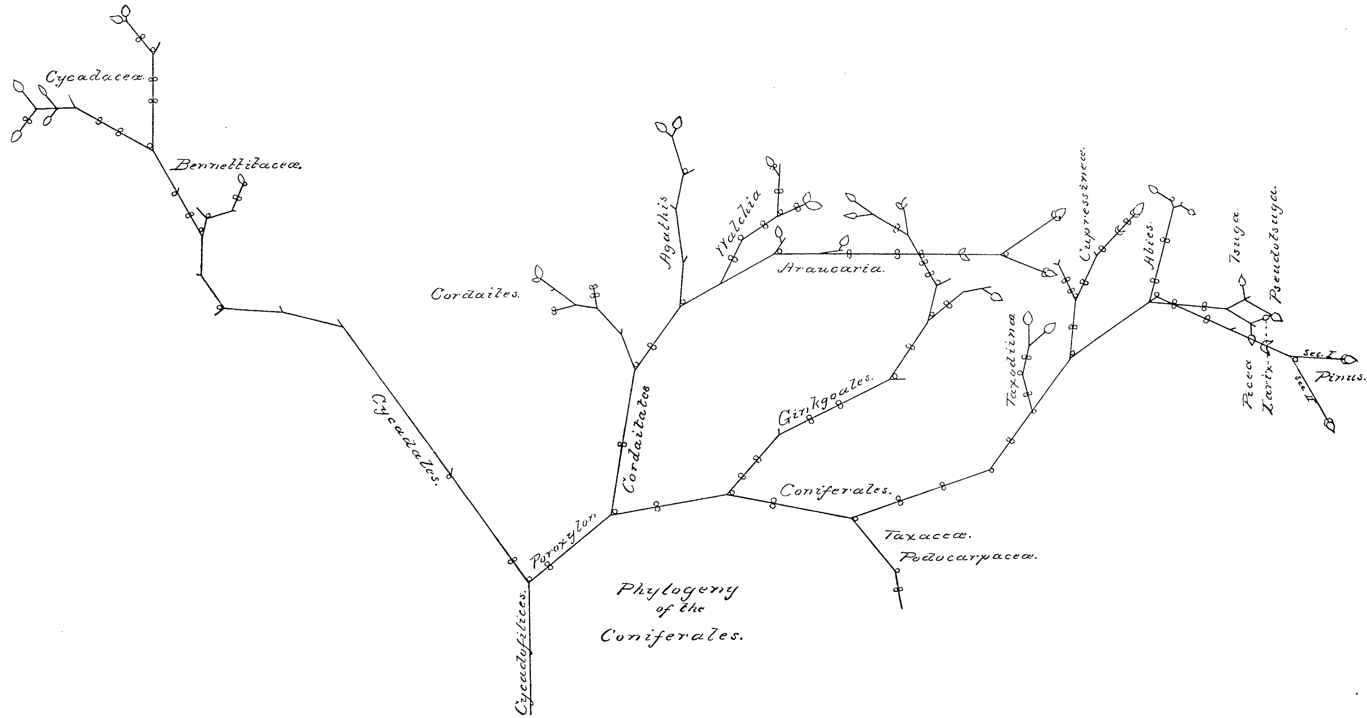


Curves for sequence of genera and frequency of anatomical characters, of the Cordaitales, Ginkgoales and Coniferales. A = Sequence of genera. B = Specific characters. C = Generic characters.

ment which in its final form is best expressed by a biological tree. A figure of this sort is difficult to construct, and there is no agreement among investigators as to the particular form it should take. While the figures in common use indicate a certain relationship in descent, they completely fail to convey any impression of the way in which the succession arises, and they furnish no indication of possible gaps. They therefore constitute a very poor working basis.

I have long been accustomed in teaching to compare the various lines of descent among plants with the branchings of a deliquescent tree, since it has always seemed reasonable to suppose that the laws which govern the branching of a limb, which give rise to all the varying forms of arrested development, and which thereby determine a particular modification of the figure which would otherwise result from unmodified growth, must be equally applicable to the general evolution of the higher forms of plants from a common ancestral type. In endeavoring to secure a natural growth which would best express all the conditions involved, a sympodium was first of all suggested, inasmuch as it conveys the idea of succession through lateral members in such a way as to indicate the direct line of descent. But sympodia as we usually know them fail to adequately express the idea of arrested development and suppression in their various forms. In the branching of *Acer platanoides* all the conditions appear to be met in a very satisfactory manner. The branch of the Norway maple, when of vigorous growth, is a monopodium, and it is obvious that such would not answer the object in view, since its most prominent feature would suggest the idea of a continuous series of coterminous members from which lateral members would arise at intervals. There is no evidence that any phylum represents such a series; on the contrary there is every reason to believe that such relations do not exist among the various groups of plants.

But in those branches of the Norway maple which exhibit slow growth various forms of arrested development are manifested. These take the form of atrophied buds, or of branches in all stages of development, and there thus arises a modified monopodium which eventually becomes, in many cases at least,



Diagrammatic representation of the Phylogeny of the Coniferales.

a true sympodium. In comparing this with the monopodial branch of vigorous growth, it appears that the alterations involve more than mere suppression. In the monopodium the average angle of divergence for the lateral members is 45.3°, while for the derived form it is 34.1°. The latter will be seen to completely fulfill all conditions with respect to the development of a phylum, even to indicating the position of missing members. Selecting from this such portion as may serve the requirements of the present case, we obtain the following figure which may be held to embody our final conclusions as to the general succession of the different gymnosperms, and from it we may gather that the highest representative — Pinus — is the terminal member in the main line of descent from the Cycadofilices through Poroxylon, while from such a central line both the Cordaitales and Ginkgoales have been given off as side lines. In the construction of this figure an attempt has been made to show all normally developed buds (o) and their relative dimensions; atrophied buds (o), the position of which is recognizable; and atrophied branches (/ –) which are still visible, but it is obvious that the figure does not show many members, all evidence of the former existence of which has completely disappeared.

The general results of these investigations serve to confirm in a very striking manner the probable monophyletic origin of the Gymnosperms as already expressed by Coulter (7), while they also show that the real transition ground, at least for all but the Cycadaceæ, was probably represented by Poroxylon as indicated by Scott (52).

LITERATURE.

ANDERSON, A. P.

(1.) Ueber abnorme Bildung von Harzbehaltern. München, 1896.

(2.) Comparative Anatomy of the Normal and Diseased Organs of Abies balsamea affected with Aecidium elatinum. Bot. Gaz., XXIV, p. 309–344. (2 pl.) 1897.

BENTHAM & HOOKER.

(3.) Genera Plantarum.

BRITTON, N. L., & BROWN, A.

(4.) An Illustrated Flora of the Northern United States and Canada. N. Y., 1896. Vol. I, 49–61.

CHAPMAN, A. W.

(5.) Flora of the Southern United States. 1884.

COOPER, J. G.

(6.) Smithsonian Report, 1858.

COULTER, J. M.

(7.) The Gymnosperms and the Seed Habit. Bot. Gaz., XXVI, 153–168. 1898.

COULTER, J. M., AND CHAMBERLAIN, C. J.

(8.) Morphology of the Spermatophytes. New York, 1901.

DE BARY, A.

(9.) Comparative Anatomy of the Phanerogams and Ferns. Oxford, 1887.

ENGELMANN, GEORGE.

(10.) Botanical Works. Cambridge, 1887.

EICHLER, A. E.

(11.) Naturlichen Pflanzenfamilien. II, 6 et seq.

ENGLER, A., AND PRANTL, K.

(12.) Naturlichen Pflanzenfamilien. II, 7–127.

ENGLER, A.

(13.) Naturlichen Pflanzenfamilien. II, 24 et seq.

ESSNER, B.

(14.) Diagnosticher Werth der Anzahl und Hohe der Markstrahlen bei den Coniferen. Bot. Centralbl., XII, 407, 1882.

FISCHER, H.

(15.) Ein Beitrag zur vergleichenden Anatomie des Markstrahlgewebes und der Jahrkichen Zuwachszonen im Holzkorper von Stamm, Wurzel und Aesten bei Pinus abies, L. Flora, vol. 68, p. 263 et seq. 1885.

GOEBEL, K.

(16.) Outlines of Classification and Special Morphology of Plants. Oxford. 1887.

GOEPPERT, H. R.

(17.) Fossilen Coniferen. Leiden, 1850.

Gray, Asa.
(18.) Manual of Botany of the Northern United States. 1890.
Hartig, Georg Ludwig.
(19.) Lehrbuch für Forster. Stuttgart, 1877.
Hartig, R.
(20.) Das Holz der deutschen Nadelwaldbäume. Berlin, 1885.
Hartig, Theodore.
(21.) Anatomie und Physiologie der Holzpflanzen. Berlin, 1878.
Hooker, Sir W. J.
(22.) Flora Boreali Americana. II, 165.
Index Kewensis.
(23.)
Jeffrey, E. C.
(24.) The Comparative Anatomy and Phylogeny of the Coniferales. Part I, The Genus Sequoia. Mem. Boston Soc. Nat. Hist. 1903.
Kalm, P.
(25.) Travels in North America. II, 646.
Knowlton, F. H.
(26.) A Revision of the Genus Araucarioxylon of Kraus, with compiled descriptions and partial synonymy of the Species. Proc. U. S. Nat. Mus., XII, No. 784, 601–617. 1890.
Macoun, John.
(27.) Catalogue of Canadian Plants. Exogens. Geol. Surv. of Can. 1883.
(28.) Rept. Geol. Surv. Can., 1875–76. 211.
Masters, Maxwell T.
(29.) Notes on the Genera of Taxaceae and Coniferae. Jn'l Linn Soc., XXX, I.
(30.) The Cypresses of Monterey. Garden & Forest, VII, 298.
Mayr, H.
(31.) Waldungen von Nordamerika. München, 1890.
Michaux, A.
(32.) Flora Boreali Americana. II, 1820.
Michaux, F. A.
(33.) The North American Sylva. III.
Muller, N. J. C.
(34.) Atlas der Hölzstructur. Halle, 1888.
(35.) Botanische Untersuchungen. Heidelberg, 1872.
Murray, A.
(36.) Edinburgh New Phil. Jn'l. n. ser. I.
Nördlinger, H.
(37.) Die Technischen Eigenschaften der Hölzer. Stuttgart, 1860.
Nuttall, T.
(38.) The North American Sylva. III.

PENHALLOW, D. P.
(39.) Taxaceae and Coniferae. Trans. R. Soc. Can., II, iv, 33–57. 1896.
(40.) North American Species of Dadoxylon. Trans. R. Soc. Can., VI, iv, 51–79. 1900.
(41.) Notes on Tertiary Plants. Trans. R. Soc. Can., IX, iv, 33–95. 1903.
PIERCE, J. G.
(42.) Studies on the Coast Redwood. Cal. Acad. Sc., II, 83–106, 1901.
POTONIE, H.
(43.) Lehrbuch der Pflanzenpalæontologie. Berlin, 1899.
PRANTL, K.
(44.) Naturlichen Pflanzenfamilien. II, 33–40.
PURSH, F.
(45.) Flora Americana. 1816.
ROTH, FILIBERT.
(46.) Timber Pines of the Southern United States. U. S. Dept. of Agric., Div. of For., Bull. 13, 133–143.
RUSSOW, E.
(47.) Zur Kenntniss des Hölzes, insonderheit des Coniferenhölzes. Bot. Centralbl., XIII, 29. 1883.
SARGENT, C. S.
(48.) Forest Trees of North America. Tenth Census of the U. S., IX. 1880.
(49.) The Silva of North America. X, XI, XII. Boston, 1897.
SCHROEDER, J.
(50.) Holz der Coniferen. Dresden, 1872.
SCOTT, D. H.
(51.) The Anatomical Characters presented by the Peduncle of Cycadaceae. Ann. Bot., XI, 399–419. 1887.
(52.) Studies in Fossil Botany. London, 1900.
SEWARD, A. C. AND GOWAN, J.
(53.) The Maiden Hair Tree. (Ginkgo biloba, L.) Ann. Bot., XIV, 109–154.
WATSON, SERENO.
(54.) Botany of California. II. 1880.
WEISS, G. A.
(55.) Anatomie der Pflanzen. Wien, 1878.
WILLIAMSON, W. C.
(56.) On the Structure and Affinities of some Exogenous Stems from the Coal Measures. M. Mic. Jn'l, II, 66–72.
WITTSTEIN, G. C.
(57.) Organic Constituents of Plants, trans. by Baron F. von Mueller. Melbourne, 1878.
ZEILLER, R.
(58.) Eléments de Palæobotanique. Paris, 1900.